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AGONISM IN ASTEROIDS

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In general sea stars have been said to be "slow-moving creatures that lie or cling to the substrate most of the time, and move about only intermittently to search for food or to avoid some physical stress" (Feder and Christensen, 1966, page 92). In regard to the sea stars *Pisaster ochraceus* and *Leptasterias hexactis*, Menge and Menge (1974, page 208) state, "It is not surprising that intraspecific aggression is nonexistent with these behaviorally simple animals." However, sea stars do pursue and catch moving prey, dig for clams, feed on particulate matter, lurch forward onto prey, or actively defend themselves against predation or cannibalism (Mauzey, Birkeland, and Dayton, 1968). Moreover, sea stars, like other echinoderms, may be capable of complex "social behavior." Reese (1966), defining social behavior as interactions between individuals as opposed to "non-social behavior" resulting from individual interaction with the physical environment, concluded that echinoderms are not capable of social behavior other than that related to reproductive activities. This conclusion was challenged by Brun (1969), and Warner (1971) with respect to brittlestar aggregations; by Dix (1969), and Pearse and Arch (1969) regarding urchin aggregations; and by Branham, Reed, Bailey and Caperon (1971), and Goreau (1964) regarding sea star distribution. Goreau (1964, page 25) thought *Acanthaster planci* to be territorial in distribution, noting "a brief transitory association" of two individuals on two occasions. Although the above authors indicate the existence of echinoderm social behavior not related to reproductive activities, only Pearse and Arch (1969) describe specific interactions between individuals that might contribute to such social behavior.

Intraspecific agonistic encounters involving ray contact between individual sea stars may reflect complex social behavior. Such encounters, here referred to as bouts, have been observed in Monterey Bay, California in all three living orders of asteroids: Forcipulata (*Pycnopodia helianthoides*, *Leptasterias hexactis*, and *Pisaster giganteus*); Spinulosa (*Patiria miniata*); and Phanerozonia (*Dermasterias imbricata* and *Mediaster aequalis*), and interspecific bouts were seen between *Pycnopodia* and two species of *Pisaster*, *P. giganteus* and *P. brevispinus* (Wobber, 1974). Sea star bout behavior therefore may be widespread, perhaps affecting the way many species feed and are distributed. This paper describes the agonistic bouts as seen in the sea stars *Patiria* and *Pycnopodia*.

Materials and Methods

Field observations resulting from about 240 hours of scuba diving between 1971 to 1974 were done in a 75 × 40 m study area on the seaward side of the U. S. Coast Guard breakwater at the southwest end of Cannery Row, Monterey, California. Depths ranged from 3–19 m. Observations were made on the large boulders forming the breakwater, and on the gently sloping sand bottom at its base as well as in aquariums. Undersea observations were recorded on plastic writing boards and by still or motion pictures, the latter augmented with time lapse series analyzed frame-by-frame (see Wobber, 1974, for further details).

Bouts were initiated by placing fresh but dead market squid, *Loligo opalescens*, a natural food for sea stars in the study area (Wobber, 1973), on the reef in weighted net bags and allowing sea stars to converge upon it; by squirting beef broth (Swanson brand) between two stationary sea stars; or by placing sea stars within 1 cm of one another.

Sex determination

Gonads from pairs in a bout were inspected to determine sex, testes were identified by their pale color, and ovaries by their pink or orange color. Since *Patiria* show an ill-defined breeding period and seem to spawn at all times of the year (Farmanfarmaian, Giese, Boolootian and Bennett, 1958), surveys of this species during May and June were considered typical distributions, not influenced by any type of sexual aggregation.

Sensitivity to ray contact

Stationary sea stars in a natural state were touched on various parts of the rays and aboral surface by diver-held sea stars and reactions of the "contacted" animals noted.

Bout outcome determination

Specimens of *Patiria* placed within 1 cm of one another will move toward one another and engage in bouts. A series of experiments was designed in which two sea stars were moved to a different, but nearby, location, placed within 1 cm of one another, and bout outcomes recorded; starting positions were marked with plastic pegs.

Convergent feeding

To determine how sea stars approach and feed upon large food items, a series of tests, termed target tests, were made on the sandy bottom at 19 m on a plastic tarpaulin which had been marked by painting 4 concentric circles at 20 cm intervals. Bait was placed within the center circle and varying numbers of conspecific individuals spaced at equidistant intervals around the outer edge of the largest circle. Each test ran 22 minutes.

Results

Intraspecific bouts, Patiria miniata

Bouts between specimens of *Patiria* seemed related to food gathering, but took place even when feeding was not obvious. The mean duration time of 52 timed bouts was 28 minutes with a standard deviation of 24.5 minutes, and a range of 3–120 minutes. On rare occasions bouts lasted more than two hours.

Ray movements during bouts can be described by the following motions or positions: (1) *extracting,* the withdrawal of a ray from beneath the opponent without a general withdrawal of the whole animal; (2) *lifting,* the raising of a ray to a position above the aboral surface of the opponent; (3) *holding,* the holding of a ray in a position above the aboral surface of the opponent; (4) *feinting,* the slight lowering and raising of the ray when in the holding position; (5) *arching,* the holding of a ray, further back than in the holding position, in a position above the sea star's own aboral surface, often with a ray in an 'S' confirmation (Fig. 1); (6) *dropping,* the lowering of a ray toward the opposing sea star; (7) *reaching,* the stretching of a ray out onto the aboral surface of the opposing sea star after a dropping motion; (8) *pushing,* the forcing of the distal end of a ray against the distal end of the ray of the opponent, often folding the tip of the ray over the opponent's ray (Fig. 2); and (9) *locking,* the surrounding and pressing in of two rays of one animal on one of the other animal's rays (Fig. 3). Two or more specimens of *Patiria* in locking positions often share the same food item.

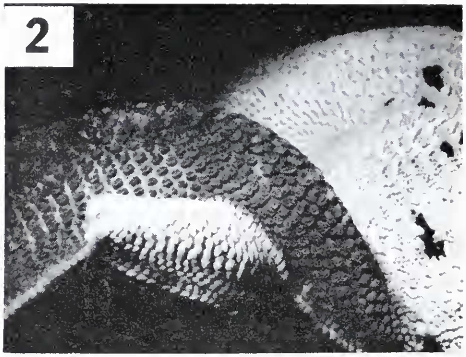
The above activities are not necessarily independent acts, but describe parts of what can be a continuous motion, graceful, fluid, and variable, and possibly dependent upon the reactions and position of the opposing sea star. It was common to see specimens of *Patiria* with facing rays in holding positions, poised without contacting one another, for long intervals. Two specimens of *Patiria* with facing rays in holding positions remained completely out of physical contact for 7.7 minutes, although ray contact both preceded and followed this period of non-contact.

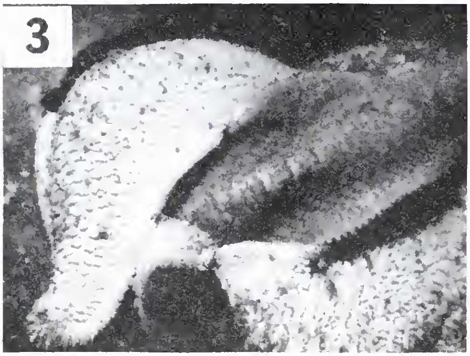
Holding or arching and the time and height of these positions often determined ray dominance: once contact was resumed the last ray to drop generally landed on top of the ray or body of the opponent, an apparent advantage. When animals were out of contact, the holding position was often lower than when in contact, sometimes even horizontal.

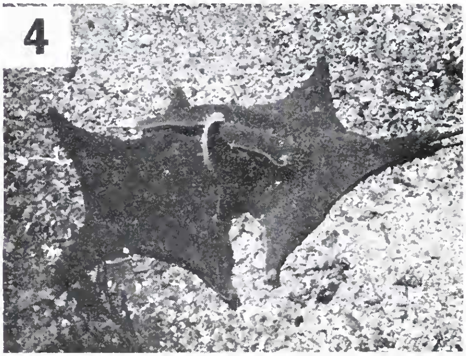
Bouts were seen to terminate by withdrawal of one or both animals, or locking or settling down near one another, often with rays overlapped, the latter taking place only when food items were involved. Bouts continued throughout feeding. Extensive pursuit in this species was not noted.

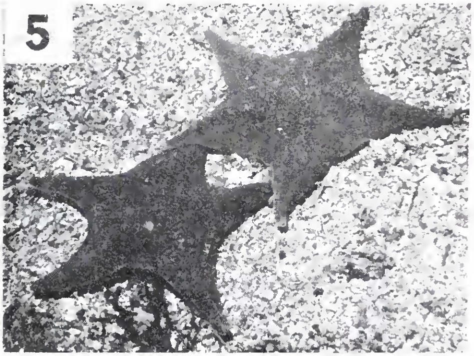
Two distinct types of bouts between specimens of *Patiria* were recorded: (1) *continuous-contact,* during which the animals maintain contact throughout, engaging multiple rays and moving their bodies against one another (Fig. 4) and, if one animal is pushed off balance or otherwise disadvantaged, the other generally follows up by actions such as a dominant two-ray advance (Fig. 5), which initiates opponent withdrawal; and (2) *intermittent-contact,* during which the animals maintain bout positions although out of contact much of the time (Fig. 1). Intermittent-contact bouts showed a tendency toward non-contact in the later stages. In five such bouts, pairs were out of contact with one another a combined mean of 51.5% of the time during the first half of the bouts and 78.5% of the time during the second half (Table I).

During intermittent-contact bouts facing rays often touched one another briefly, the aboral surface of one sea star's ray tip contacted by the oral surface of the other sea star's ray tip. This contact initiated a swift raising of the rays of both individuals, the ray touched on its aboral surface going into the arching or holding position, the ray of the opponent assuming a lower hold position (Fig. 1). Within









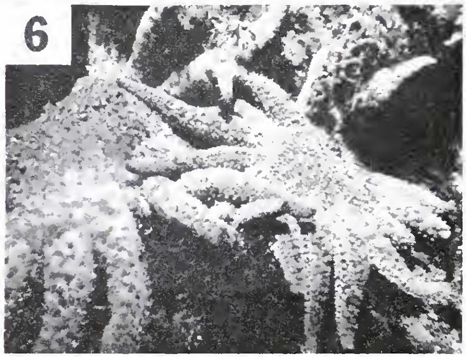


FIGURE 1. Specimens of *Patiria* engaged in an intermittent-contact bout; sea star on left with facing ray in arching position, sea star on right with facing ray in holding position.

FIGURE 2. Specimens of *Patiria* showing the detail of rays in the pushing position during an intermittent-contact bout.

FIGURE 3. Specimens of *Patiria* in locking position; sea star on right with two rays surrounding one ray of sea star on the left.

FIGURE 4. Specimens of *Patiria* engaged in a continuous-contact bout.

FIGURE 5. Specimens of *Patiria* engaged in continuous-contact bout; sea star at right in two ray dominant advance, sea star on left withdrawing.

FIGURE 6. Specimens of *Pycnopodia* engaged in intraspecific bout.

TABLE I

Non-contact time within five Patiria miniata *intermittent-contact bouts recorded by time lapse motion pictures.*

Bout	Duration in minutes	% non-contact time		
		Total	First half	Second half
1	90	53.5	28.5	78.7
2	84	80.8	67.4	94.2
3	72	88.5	79.5	97.8
4	20	20.9	9.6	32.2
5	17.4	81.0	72.4	89.7
$\bar{x} \pm$ s.d.	56.7 ± 35.3	64.9 ± 28.0	51.5 ± 30.7	78.5 ± 26.9

the 5 bouts shown in Table I, a combined total bout time of 283.4 minutes, such a sequence was seen 35 times ($\bar{x} = 7.0 \pm 2.9$ s.d., range 2–9). Termination of intermittent-contact bouts usually followed the pattern of a dominant two-ray advance which appeared to initiate opponent withdrawal (Fig. 5).

Primary ray positions of bouts were classified into three categories: advantageous; neutral; and disadvantageous, depending on the ray's relationship to the opponent's facing ray(s), *i.e.,* in a dominant position the ray was either touching the opponent's aboral surface or in a higher position than the opponent's ray(s), and thus able to descend on top of the opponent. Holding positions were separated into three categories depending upon the ray's position relative to the horizontal: high hold, 60° to 90°; medium hold, 30° to 60°; and low hold, from horizontal or below to 30°. Acts such as reaching and feinting were not considered in these data. Intra-individual sequence patterns of the above acts were taken from time lapse motion pictures of three intermittent-contact bouts of *Patiria* and translated into frequencies of occurrence (Table II, Fig. 7). One action sequence was the subordinate ray touch which led to an arching position 69% of the time or a high hold position 31% of the time. Trends in a given bout toward overall dominant-subordinate relationships of individual sea stars were not established. Cannibalism was not observed in *Patiria.*

Specimens of *Patiria* in intermittent-contact bouts can engage two opponents simultaneously and cause withdrawal of both.

Intraspecific bouts, Pycnopodia helianthoides

Bouts occurred when two sea stars came in contact, whether feeding or not. Although no quantitative data were taken of approximately 50 bout observations, durations of most were estimated to be less than two minutes. The longest observed bout lasted about 10 minutes.

A ray movement position unique to *Pycnopodia* is *side-slipping,* the semi-horizontal sliding of rays between, then over and onto the rays of the opponent, sometimes accomplished by a rotating of the whole body clockwise or counterclockwise. *Pycnopodia* did not engage in feinting, pushing, or locking positions. Up to seven rays of one sea star may be involved in one bout at a given time.

TABLE II

Frequencies of intra-individual two-act agonistic sequences from intermittant-contact bouts of three Patiria *pairs where one ray each of each pair of sea stars was involved. Observed frequencies in each row are figures on top, figures below in parentheses indicate percent occurrence of following act. (Columns add to 100 ±).*

Following Act	INITIAL ACT										
	Advantageous				Neutral			Disadvantageous			
	Arching	Dominant ray touch	High hold*	Base ray contact**	Pushing	Both base ray contact	Extracting	Subordinate ray touch	Medium hold††	Low hold†	Base ray con-tacted
Arching	0	0	1 (02)	3 (16)	0	1 (20)	0	20 (69)	1 (04)	1 (06)	3 (38)
Dominant ray touch	9 (29)	0	15 (34)	0	0	0	0	0	2 (08)	3 (17)	0
High hold	1 (03)	16 (55)	0	6 (32)	3 (50)	0	1 (33)	9 (31)	7 (29)	1 (06)	2 (25)
Base ray contact	7 (23)	1 (03)	3 (07)	0	2 (33)	1 (20)	1 (33)	0	3 (13)	1 (06)	0
Pushing	2 (06)	0	1 (02)	1 (05)	0	0	0	0	0	2 (11)	0
Both base ray contact	1 (03)	0	0	1 (05)	0	0	1 (33)	0	1 (04)	0	0
Extracting	0	0	0	0	0	1 (20)	0	0	0	0	3 (38)
Subordinate ray touch	2 (06)	0	12 (27)	1 (05)	0	0	0	0	6 (25)	7 (39)	0
Medium hold	4 (13)	9 (31)	5 (11)	5 (26)	0	0	0	0	0	1 (06)	0
Low hold	5 (16)	3 (10)	5 (11)	1 (05)	0	2 (40)	0	0	2 (08)	0	0
Base ray contacted	0	0	2 (05)	1 (05)	1 (17)	0	0	0	2 (08)	2 (11)	0

*Disadvantage 57.7% **Disadvantage 37% †Advantage 22% ††Advantage 21%

Initial ray touching, extracting, lifting, holding, arching, dropping, and reaching are part of the bout, but ray movements are faster than the ray movements of *Patiria*.

In most bouts observed, initial contact was a touching of the distal ends of the rays by both individuals, followed by a pulling upwards or backwards of the contacted rays. An approaching sea star sometimes hesitated and raised its rays, or slid its rays over or between the facing rays of the other animal. Individuals have not been seen to move completely on top of one another. Once initial contact was made, the body of a sea star generally maintained its position as it withdrew one or more rays at a time and placed them on the aboral surface of the other sea star. It was not unusual to see both individuals engaged in extracting rays in this manner and then laying them down on one another's surface simultaneously.

During bouts, sea stars were in continuous contact with one another (Fig. 6). Neither pedicellariae nor tube feet were used for adhering to or defending against the opponent. Withdrawal appeared to be initiated by the extent to which one or more rays were successfully placed on the aboral surface of the opponent: the closer to the center of the disc, the greater the reaction. Bout outcomes resulted in the withdrawal of one or both animals, or the pursuit of one by the other. Pursuit distances up to 3 m were recorded. If only one individual withdrew, the withdrawn animal sometimes stopped 10–100 cm away, raised the rays which were facing the other animal and approached directly again. The returning sea star immediately initiated another bout by moving its raised facing rays onto the opponent's aboral surface. Bouts between specimens of *Pycnopodia* did not terminate in overlapping or settling down in contact with one another, even over large items of food.

An individual may engage two or more opponents in bout behavior, employing several groups of rays around its periphery simultaneously.

Interspecific bouts

Interspecific bouts were seen between specimens of *Pycnopodia* and specimens of two species of *Pisaster*, *P. giganteus* and *P. brevispinus*. Five such bouts involved a specimen of *Pycnopodia* attacking a feeding specimen of *Pisaster* sp. Six additional bouts were initiated by feeding dead *Loligo opalescens* to either species of *Pisaster*. In all bouts a specimen of *Pycnopodia* approached and placed some of its facing rays on the aboral surface of the feeding *Pisaster* individual, removing the rays almost immediately in a continuous "flailing" motion, while reaching beneath the feeding sea star with other rays, often thus obtaining some or all of the food. The attacking animal's rays were fastened onto by the pedicellariae of the specimen of *Pisaster* which raised and twisted its facing rays causing the aboral surface bearing the pedicellariae to come down on the aboral surface of the attacking animal. The specimen of *Pycnopodia* repeatedly withdrew its rays, but did not use its own pedicellariae. These encounters lasted approximately 30 seconds. When the *Pycnopodia* individual withdrew, its facing rays were sometimes shortened and thickened, the tips of many curled back over themselves, appearing temporarily immobile, as though paralyzed. On two separate occasions a specimen of *Pisaster giganteus* feeding on a large dead fish was approached by a specimen of *Pycnopodia* and the animals engaged in a bout. Both times the specimen of *Pycnopodia* withdrew although one specimen of *Pycnopodia* was 40 cm in diameter and its opponent 28 cm in diameter.

Specimens of *Patiria* were often touching or being touched by specimens of *Pycnopodia* or*Pisaster* sp., either incidentally or on food, but no interspecific agonism was observed.

Sex determination

Sex differences between 19 arbitrarily chosen pairs of *Patiria* in a bout did not show significant deviation from chance ($P > 0.70$, d.f. = 2), therefore bouts are apparently not a sexual behavior. As *Pycnopodia* populations were sparse, gonadal material was not checked in this species.

Sensitivity to ray contact

Hand-held specimens of 10 *Pycnopodia* 6 cm in diameter touched to the aboral surface of 10 stationary animals 45 cm in diameter initiated no withdrawal responses, whereas 10 specimens of the same or larger size initiated withdrawal in all cases, the response appearing more intense as the stationary animal was touched closer to the center of the disc. Touching on the madreporite did not elicit unusual withdrawal responses. Reactions of specimen pairs of *Patiria* tested in the above manner were so slow that results were uncertain.

Bout outcome determination

The following observations were performed only with specimens of *Patiria* as any handling or manipulation of specimens of *Pycnopodia* appeared to affect subsequent responses.

Size. Nine pair of sea stars were selected; one member of each pair being over 16 cm and one being under 13 cm in diameter. Each pair was placed with rays closest to the madreporite opposing one another. Of the nine bout outcomes, four large and five small specimens of *Patiria* withdrew; tested size differences therefore were not significant ($P > 0.70$, d.f. = 1).

Madreporite position. Opponent madreporites were not directly attacked, nor did the touching of a madreporite by an opponent initiate withdrawal. However, of 21 pairs tested for bout outcomes, 18 with the madreporite toward the opponent and 3 with the madreporite away from the opponent withdrew. The Chi-square value of 10.72 ($P < 0.005$, d.f. = 1) indicates that madreporite position is a highly significant factor.

Area recognition. Two experiments were designed to determine whether *Patiria* individuals might have a behavioral bout advantage by virtue of "recognition" of the area beneath them (thus indicating territoriality).

In the first experiment, two animals of similar size were moved at the same time, the same approximate distance through the water. One, the "replaced" sea star, was set down on the same spot from which it had been removed; the other, the "transported" sea star, was placed 1 cm from the closest ray of the replaced animal, positioned madreporite-to-madreporite. Of 14 trials, only one replaced sea star withdrew. Chi-square was highly significant ($P < 0.005$, d.f. = 1) and territoriality is strongly supported.

In the second experiment, to determine whether the obvious advantage to the replaced sea star was due to area recognition or related to disturbed sand on which the animal was placed, two specimens of *Patiria* of similar size were moved as above, but in this series, one animal was placed on the area from which the other sea star had just been lifted, and the other placed alongside. Out of 9 trials, 5 animals placed alongside the disturbed area and 4 placed on the disturbed area withdrew (Chi-square = 0.12, $P > 0.70$, d.f. = 1), suggesting that the disturbed area itself is not a factor in the outcome.

Area recognition vs. *size or madreporite position.* In tests of 9 bout pairs where the replaced sea star was either larger or smaller (within a 3 cm variation), all transported animals withdrew. In similar tests of 10 bout pairs, madreporite position being the variable, all transported animals withdrew, indicating a high degree of territoriality regardless of relative body orientation or size variation of the magnitude tested.

Convergent feeding

Three target tests (see materials and methods) were carried out to determin how individuals of *Patiria* converge on large food items. Fresh animals were used for each test. Rays closest to the bait at the start of the tests became the leading rays in movement toward the bait. Specimens of *Patiria* first to arrive at the bait engaged in bouts with one another and approaching individuals, even-

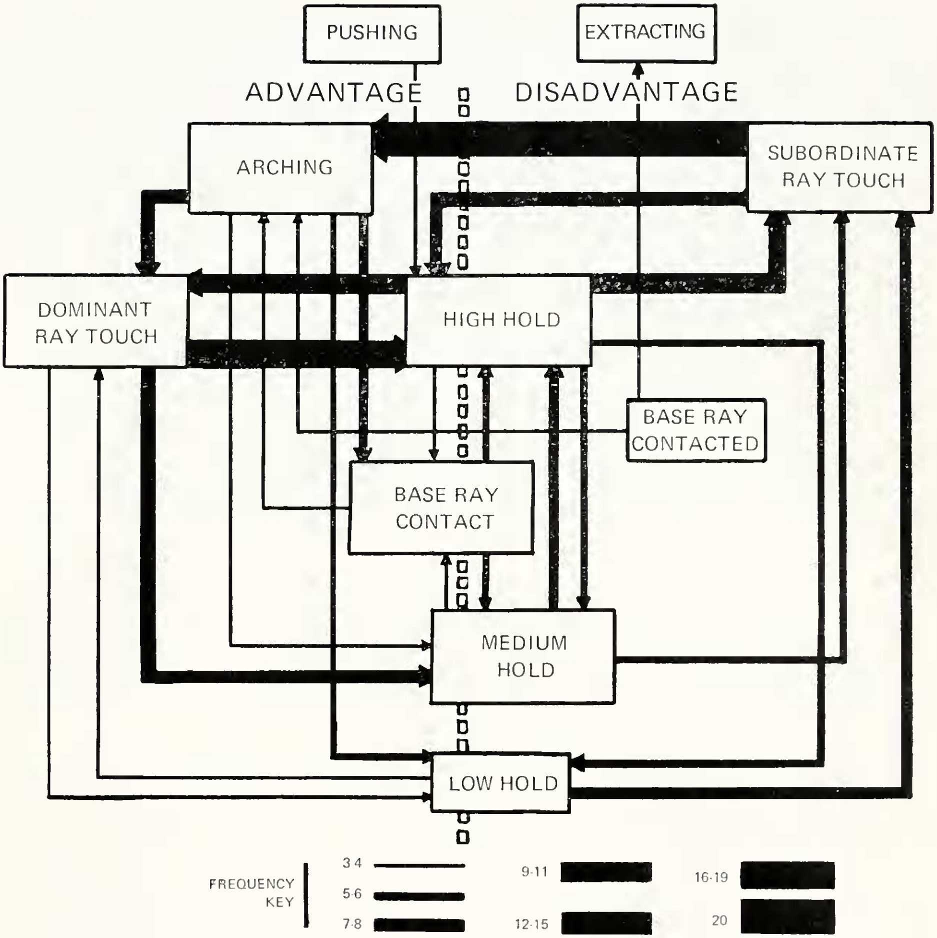


FIGURE 7. An agonistic sequence diagram of *Patiria* intermittent-contact bouts derived from observed frequencies in Table II. Thickness of lines indicates frequency of occurrence, and arrowheads indicate direction of the sequence. Items to the left of the dashed line have a bouting advantage, to the right a disadvantage. Frequency values 1 and 2 were eliminated for simplification.

tually covering the bait and driving latecomers away. After 22 minutes, the number of animals on the bait was approximately the same regardless of the starting group size (Table III). In the starting groups 10, 18, and 26; 90%, 83% and 80.8% respectively either reached the bait or engaged in bouts with animals on the bait. The more animals in the starting group, the more subsequent movement away from the bait by withdrawing animals. Of those withdrawn, 71.7% were recorded as engaged in bouts on the tarpaulin where there was no possibility of food.

TABLE III

Target test results showing dispersal of three variable quantity test groups of Patiria *around a fixed bait after 22 minutes. Figures in parentheses represent sea stars which were not on bait but were engaged in bouts.*

Test	Number of sea stars	Distribution (distance from bait)						Total not on bait	% bouts not on bait
		On bait	0 to 20 cm (not on bait)	20 to 40 cm	40 to 60 cm	60 to 80 cm	Over 80 cm		
1	10	6	1 (1)	2 (2)	—	—	1 (?)	4 (3)	75
2	18	5	4 (4)	4 (4)	2 (2)	—	3 (?)	13 (10)	77
3	26	7	3 (3)	4 (4)	5 (4)	2 (1)	5 (?)	19 (12)	63
		Total % engaged in bouts and not on bait							71.7

Population data

Percentage of sea stars engaged in bouts. Because *Pycnopodia* bouts were rarely seen (less than 1 bout for every 10 hours of diving), no estimate was made of the percentage of bout pairs. *Patiria* bouts were extremely common. Counts

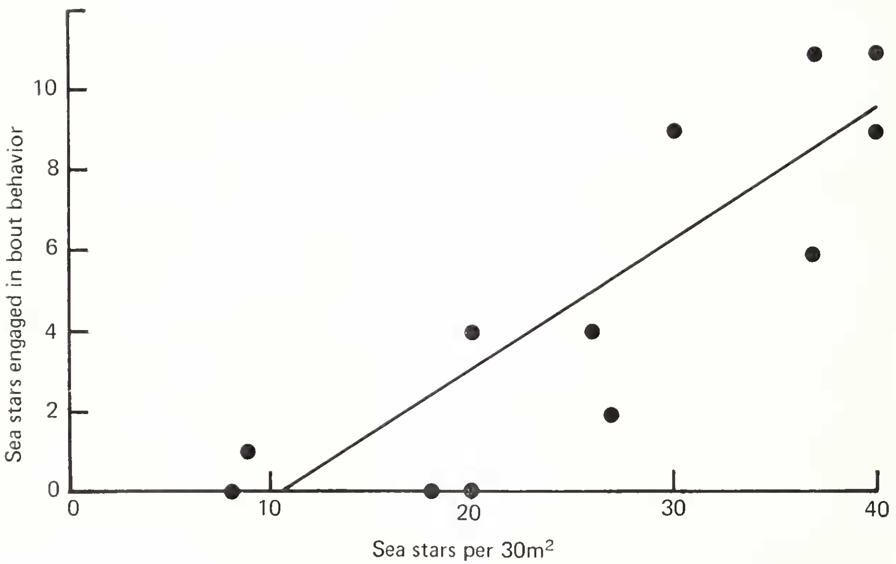


FIGURE 8. Relation of sea star density to bout behavior in 12 2 × 15 transect surveys of *Patiria* ($r = +.86$).

on the exposed surfaces of the large rocks that form the breakwater from three different locations of 30 m^2 at 09:00, 11:00, and 14:00 hours showed that of a total of 389 individuals, a mean of 23.7% were engaged in bouts, s.d. $\pm$ 4.09%, range 19.0–26.6%. From this sampling, of the total of those individuals engaged in bouts, 93.7% were engaged in the intermittent-contact type of bout and the remainder were engaged in the continuous-contact type of bout. Although no quantitative data were taken, *Patiria* bouts appear to continue nocturnally at approximately the same level. Twelve 2×15 m transect surveys taken on the sandy bottom in the study area indicated an increase in bout activity with increasing density (Fig. 8).

Dispersion surveys. Subtidal population distribution data was impractical for *Pycnopodia* because of the sparse population (0.013–0.1015 per m^2). *Patiria* dispersion data were taken on the sand at the base of the breakwater during May and June of 1972, from areas where convergent feeding did not seem to play a part. The combined total area of all surveys was 410 m^2. Analysis was made in regard to randomness and the data were fitted to a Poisson distribution, resulting in a Chi-square value of 96.3. The hypothesis that the animals are distributed randomly was rejected ($P < 0.0001$, d.f. $= 2$). Since the ratio $s^2/\bar{x} = 2.43$ is greater than unity, it was concluded that individuals of *Patiria* exhibit contagious distribution.

Discussion and Conclusions

The results demonstrated that agonistic bouts are an important social behavior in regard to *Patiria* and *Pycnopodia*. There are major differences in intraspecific bout behavior between the two species. *Patiria* bouts seemed less aggressive, mostly of the intermittent-contact type where both individuals were out of physical contact for long periods of time, occasionally terminating in food sharing. A withdrawing individual was not pursued extensively. *Pycnopodia* bout outcomes were quick and decisive, the winner maintaining food or area, and sometimes pursuing the loser for distances up to 3 m.

In interspecific bouts between specimens of *Pycnopodia* and *Pisaster* sp., dissimilar behaviors were used by each species. Pedicellariae, used only by specimens of *Pisaster*, seemed to initiate withdrawal of the opponent, temporarily immobilizing its rays, a behavior which allowed specimens of *Pisaster* to compete with the larger, more active sea star, perhaps a more important function for pedicellariae than the occasional capture of food as described by Feder and Christensen (1966) and Robilliard (1971). Menge and Menge (1974) report use of pedicellariae by *Pisaster ochraceus* in aggressive behavior against *Leptasterias hexactis*.

I saw no indications of cannibalism as reported by Mauzey *et al.* (1968) and Greer (1961) for *Pycnopodia*. The non-predatory intraspecific bouts I observed may have evolutionary roots in intraspecific competition rather than in cannibalism. However, Mauzey *et al.* (1968) describes the use of the rays in cannibalistic fighting, so intraspecific bouts cannot be assumed to be a universally harmless means by which sea stars confront one another.

It is not clear why a specimen of *Patiria* with its madreporite closer to the opponent is at a bout disadvantage: the difference in adult size was not significant (although the animal with the longest reach should logically be more of a threat to the opponent's madreporite); the madreporite was not directly attacked nor did the touching of it in itself cause withdrawal. Bout differences regarding body orientation may have more to do with the rays themselves than the relative position of the madreporite: rays adjacent to the madreporite may be more sensitive than other rays and therefore at a disadvantage. Selective advantages to such ray differentials are not apparent. Kjerschow-Agersborg (1922) claims that in *Pycnopodia* the rays adjacent to the madreporite lead during locomotion, a factor that could be related to differential ray sensitivity, however, observations during this study indicated that neither *Pycnopodia* nor *Patiria* rotate the body to change direction nor favor certain rays as leading rays.

Noble (1939) presented a general definition of territory as "any defended area." The animal defending territory usually "wins" by driving away conspecifics (Tinbergen, 1952). My results suggest that a territorial behavioral advantage exists in *Patiria* populations which outranks an advantage in body orientation in regard to ray or madreporite positions.

Woolf (1968, page 283) states that animals exhibiting territoriality follow a uniform rather than a contagious distribution pattern. The contagious distribution demonstrated by populations in the study area may be due to the length of time spent in individual bouts and the high per cent of sea stars so engaged, even though bout outcomes may finally result in spacing-out. Target tests illustrated this (Table II). Specimens of *Patiria* converged on the bait; however, once it was covered, late comers withdrew. The majority of the withdrawn animals did not disperse evenly but, at least temporarily, engaged in bouts with one another, even in the absence of food.

Pycnopodia bouts generally terminated rapidly with one or both animals withdrawing, even over food; therefore, bout behavior appeared to space-out individuals of this species.

Bout abilities may be selected for in competitive situations because the winner retains possession of the food, grows larger, uses less energy in food search, better survives when food is scarce, and thus produces more progeny. The spreading effect of the sea stars which withdraw from bouts may result in all the individuals of the population utilizing food more evenly.

Continuous-contact *Patiria* bouts appeared to require a large degree of individual effort. As up to 26.6% of the individuals in a *Patiria* population were engaged in bouts, it would not be surprising that intense forms of this activity would tend toward modification. Modification to intermittent-contact would have certain advantages: (1) lower energy utilization; (2) the possibility of feeding while engaged in a bout; (3) the ability to bout with two animals simultaneously (perhaps impossible in continuous-contact bouts in this species); and (4) quick withdrawal from the bout by either animal at any time.

Within intermittent-contact bouts, contact decreased with time, pointing to mechanisms which reduce the effort involved over time, such as habituation or short term learning as demonstrated in *Pisaster giganteus* by Landenberger (1966). A complex level of communication may be indicated both by a progression toward less contact, and by common sequence patterns which elicit specific changes in the behavior of recipient animals (Dingle, 1969). Differences within the two types of bouts, such as change of intensity, exaggeration of components (*e.g.,* in intermittent-contact bouts, pushing with the distal ends of rays in contrast to whole body pushing in continuous-contact bouts), and other factors, imply a pattern of signal movements derived through a process of ritualization, as reviewed by Blest (1961). Blest (1961, page 102) hypothesized that, "in the course of evolution, both locomotory movements and acts (concerned with comfort, heat-regulation, and capture of prey) have been selected and modified to produce signals. Such movements have been termed 'derived' and may exist alongside their ancestral activities." The evolutionary development by which such movements have arisen has been called "ritualization" by Tinbergen (1952).

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Summary

1. Intraspecific agonistic behavior, called bouts, which involves ray interactions between individual sea stars, is reported in species from all three living orders of asteroids and described for *Patiria miniata* and *Pycnopodia helianthoides.* This behavior indicates a certain sensitivity to conspecific contact on the aboral surface, in which each individual attempts to place a ray or rays on top of its opponent, an act which may initiate opponent withdrawal. Agonistic intraspecific bouts affect the distribution and feeding of both species although bouts may take place where food is not present.

2. *Patiria* bouts may last over two hours and sometimes terminate by individuals overlapping and sharing food. Evidence suggests that *Patiria* bouts are: (a) quite common; (b) not related to sexual behavior; (c) territorial; and (d) influenced as to outcome by relative body orientation; however, when territorial behavior is involved, relative body orientation does not affect bout outcomes. *Pycnopodia* bouts are of shorter duration (up to 10 minutes), terminating with the withdrawal of one or both animals, and sometimes resulting in an extensive pursuit.

3. Two forms of intraspecific *Patiria* bouts are noted: continuous-contact and intermittent-contact. Intermittent-contact bouts appear less intensive, permitting individuals to feed and to engage in bouts with more than one opponent at a time. It is speculated that intermittent-contact bouts are a type of ritualized activity of a fairly complex nature.

4. Interspecific bouts between specimens of *Pycnopodia* and two species of *Pisaster* (*P. giganteus* and *P. brevispinus*) have been observed only when the *Pisaster* sp. is in possession of food. *Pycnopodia* individuals approach and place

rays on the aboral surface of the feeding sea star while attempting to obtain the food with other rays. The specimen of *Pisaster* sp. actively counterattacks using its pedicellariae.

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